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Original Research Article

Development of growth rate, body lipid, moisture, and energy models for white sturgeon (*Acipenser transmontanus*) fed at various feeding rates

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The objectives were to develop and evaluate: 1) growth rate models, 2) body lipid, moisture, and energy models for white sturgeon fed at various feeding rates (FR; % body weight [BW] per day) and then evaluate responses at proportions of optimum feeding rate (OFR) across increasing BW (g). For objective 1, 19 datasets from the literature containing initial BW, FR and specific growth rate (SGR; % BW increase per day) were used. For objective 2, 12 datasets from the literature (11 from objective 1) containing SGR, FR, final BW, body lipid (%), protein (%), ash (%), moisture (%), and energy (kJ/g) were used. The average rearing temperatures was 19.2 ± 1.5 °C (mean ± SD). The average nutrient compositions and gross energy of the diets were 45.7 ± 4.3% protein, 14.8 ± 3.2% lipid, and 20.4 ± 1.3 kJ/g, respectively. The logistic model was used for objectives 1 and 2 to develop a statistical relationship between SGR and FR, then an iterative technique was used to estimate OFR for each dataset. For objective 2, the statistical relationship between body lipid, energy, and moisture and FR was established. Using the OFR estimate, SGR, body lipid, energy and moisture were computed at various FR as a proportion of OFR. Finally, a nonparametric fitting procedure was used to establish relationships between SGR, body lipid, energy and moisture (responses) compared with BW (predictor) at various proportions of OFR. This allows visualization of the effect of under- or over-feeding on the various responses. When examining the differences between OFR at 100% and various proportions of OFR, SGR differences decrease and moisture differences increase as BW increases. Lipid and energy differences decrease as BW increases. To our knowledge, these are the first description of changes in nutrient compositions when white sturgeon are fed at various FR. Because physiological and behavioral properties that are unique to sturgeon, results from this study are specific to sturgeon under the conditions of this study and cannot be compared directly with salmonids even if some of the results are similar. This research provides insight to designing future nutritional studies in sturgeon.

1. Introduction

White sturgeon (*Acipenser transmontanus*) is an ecologically and commercially important species (Moyle, 2002; Lee et al., 2014). Furthermore, this species has some biological uniqueness, which is different from the commonly cultured salmonids. These differences include: 1) long life span of more than 100 years in the wild compared with 2 to 4 years in salmonids (Moyle, 2002); 2) late sexual maturity of 4 years for males and 7 to 8 years for females raised in captivity instead of 1 to 3 years in salmonids (Doroshov et al., 1997); 3) a unique fat storage organ (gonadal body fat; Scarnecchia et al., 2007; Lee et al., 2016) instead of

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viscera in salmonids; 4) and sturgeon are nibblers (Cui et al., 1997) instead of meal feeders like salmonids (for salmonids see Shearer, 1994).

Feeding rate (% body weight per day) is a major element affecting growth in fish (Brett and Groves, 1979), and thus determination of optimum feeding rate (OFR; %), defined as the rate at which growth is maximal, is critical for success of aquaculture operations. In a previous study, we demonstrated how to develop an OFR model that can predict an OFR at a given body weight of white sturgeon ranging from 0.05 to 800 g (Lee et al., 2014). The approach used previously to find an OFR at different weight classes (Lee et al., 2014) can be expanded using a different modeling approach to evaluate specific growth rate (SGR) at different body weights considering different proportions of OFR (i.e., 30% to 110% of OFR). This new approach will allow researchers to examine the feeding rate-dependent growth performance under different OFR proportions. Understanding the relative differences between proportions of OFR can also be valuable when extending this information to applied aquaculture settings.

Due to the high correlation between growth and nutrient partitioning in association with feed availability (Storebakken et al., 1991; Lee et al., 2016), developing body composition and energy models for white sturgeon at a given feeding rate will also enhance our understanding of nutrient and energy content changes in relation to feeding rate. To our knowledge, these types of models have not been developed for white sturgeon. Therefore, our objectives of the current study were development and evaluation of 1) growth rate models and 2) body compositions (lipid, moisture) and energy models for white sturgeon when fed at various proportions of OFR across increasing body weight. The current study is unique because we demonstrate dynamic relationships for these responses at various proportions of OFR for white sturgeon from first exogenous feeding to young of the year.

2. Materials and methods

2.1. Description of datasets

Nineteen datasets were used for objective 1 to describe how growth rate changed when white sturgeon were fed at increasing feeding rates and to also describe growth rate when fed at different proportions of OFR across a range of average initial body weights varying from 0.05 to about 800 g. Every dataset represents a different weight class of sturgeon. Observations taken at different feeding rates were independent from each other. The datasets were obtained from 6 published studies (Hung and Lutes, 1987; Hung et al., 1993, 1995; Deng et al., 2003; De Riu et al., 2012; Lee et al., 2016) which were carried out to evaluate the effects of feeding rate on growth performance in white sturgeon across body weights. Many of the diets that were used in the studies are commercial feeds that have been used on white sturgeon farms in California, USA. Some of them were formulated diets developed to meet nutrient requirements of white sturgeon. The average nutrient compositions and gross energy of the diets were (45.7 ± 4.3)% (mean ± SD) crude protein and (14.8 ± 3.2)% crude lipid, and 20.4 ± 1.3 kJ/g, respectively.

The 19 datasets contain initial and final body weights (g; weight class), various feeding rates (FR; % body weight per day; independent variable), and specific growth rates (SGR; % body weight increase per day; dependent variable) (Table A). Among 19 datasets in objective 1, 2 groups of datasets were dependent, i.e., datasets 9 to 12 and datasets 14 to 18 because the measurements were taken from the same set of fish at different body weight stages. However, they were treated as independent datasets due to the following reasons. Firstly, the interpretation of the results showed no difference when these datasets were pooled and considered as a single dataset. Secondly, most importantly, the second step which involved using nonparametric curve fitting using estimates from each dataset were improved dramatically due to the higher number of sample size (i.e., 19 datasets compared with 12 datasets when considering the datasets 9 to 12 and 14 to 18 were independent). Finally, insufficient data points were available such that a mixed effects model would result in variance−covariance matrix that would have an unstable structure.

Twelve independent datasets were used for objective 2 to describe how body lipid, energy, and moisture content changed when white sturgeon were fed at increasing FR and to also describe body lipid, energy, and moisture content when fed at different proportions of OFR across a range of average final body weights varying from 0.10 g to about 700 g. Again, these datasets represent different body weights. These datasets were obtained from the aforementioned published studies, except the study from Hung et al. (1995) where the fish were not slaughtered, and another study from Lee et al. (2015) which was added. Because the values of body composition and energy content were acquired through sacrificing animals at the end of a growth trial, 2 groups of the datasets from objective 1 (datasets 9 to 12 and 14 to 18) that were used in objective 2 were pooled. All fish were slaughtered in objective 2, and all datasets were independent. The 12 datasets, including average final body weights (g; weight class), various FR (%; independent variable), and body compositions (lipid, moisture; % as wet basis) and energy (kJ/g as wet basis) (dependent variables), are listed in Table 1. Protein and ash content were not considered in the current study because these 2 variables showed little change when body weight was larger than ca 30 g. All data points including moisture, protein, lipid and ash content are presented in Fig. 1.

2.2. Model development (objectives one and two)

In order to describe the relationship between various FR and response variables (e.g., growth rate, body composition and energy) for the given datasets, it was necessary to have an OFR estimate for each dataset. We defined the OFR as the rate at which growth is maximal or approaches maximal. Then the OFR can be used as a standard to examine other FR as a proportion of OFR. In our previous study (Lee et al., 2014), a prediction model for estimating an OFR for white sturgeon was developed. In summary, the OFR for the 19 datasets, which were the same datasets used in objective 1 of the current study, were estimated using a quadratic broken-line model that was selected as the best-fit model among the tested models (one-slope straight broken-line, two-slope straight broken-line, second-order polynomial models) on the basis of model selection criteria (e.g., adjusted coefficient of correlation, corrected Akaike information criterion). Then, the relationships between the 19 estimated OFR and transformed initial body weights were investigated via various regression models, and the best-fit model was a bi-exponential regression model that can predict OFR for a given body weight ranging from 0.05 to about 800 g. That modeling approach, although valid, did not capture the non-linear nature of the response. To overcome this drawback, a logistic growth curve was utilized for estimating the OFR in both objectives 1 and 2, where the FR and the SGR were the predictor and the response, respectively. Feed conversion ratio (FCR) was not used as the response because feed intake was not measured and as FR approaches OFR and beyond, more feed is wasted. Hence, the

Table 1
List of 12 datasets used to describe how body lipid, energy, and moisture content change when white sturgeon are fed at various feeding rates (% body weight per day).

Dataset (FBW,[1] g)	Source	Number of replications,[2] Duration of feeding, week	Feeding rate, %	Response variable as wet basis[3]		
				Lipid, %	Energy,[4] kJ/g	Moisture, %
1 (0.10)	Deng et al. (2003)	4, 1	10	1.53	2.32	90.0
			20	1.71	2.47	89.5
			30	1.84	2.54	89.3
			40	1.94	2.60	89.0
			50	1.93	2.61	89.0
			60	1.99	2.66	88.8
2 (0.20)	Deng et al. (2003)	4, 1	5	1.49	2.24	90.4
			10	1.93	2.51	89.5
			15	2.23	2.61	89.3
			20	2.40	2.71	89.0
			25	2.38	2.74	88.9
			30	2.40	2.73	88.8
3 (0.31)	Deng et al. (2003)	4, 1	2.5	1.28	2.15	90.4
			5.0	1.55	2.39	89.5
			7.5	1.72	2.47	89.3
			10.0	1.86	2.59	88.8
			12.5	2.07	2.64	88.8
			15.0	2.38	2.80	88.4
4 (0.65)	Deng et al. (2003)	4, 1	2.5	2.15	2.56	89.1
			5.0	2.55	2.97	87.5
			7.5	2.84	3.12	87.1
			10.0	3.28	3.30	86.7
			12.5	3.11	3.29	86.5
			15.0	3.30	3.35	86.4
5 (4.5)	De Riu et al. (2012)	4, 1	3.0	3.40	3.70	84.5
			4.0	3.75	3.77	84.5
			5.0	4.03	3.92	84.0
			6.0	4.28	3.99	84.0
			7.0	4.30	4.05	83.7
			8.0	4.35	4.06	83.7
6 (6.4)	De Riu et al. (2012)	4, 1	2.0	4.03	4.00	82.7
			3.0	4.30	4.00	83.1
			4.0	4.73	4.23	82.4
			5.0	4.95	4.29	82.3
			6.0	4.95	4.22	82.6
			7.0	5.03	4.28	82.3
7 (11.6)	De Riu et al. (2012)	4, 1	1.0	4.13	4.15	82.9
			2.0	4.63	4.39	82.2
			3.0	4.88	4.43	82.2
			4.0	5.20	4.66	81.6
			5.0	5.43	4.74	81.5
			6.0	5.38	4.80	81.3
8 (13.1)	De Riu et al. (2012)	4, 1	1.0	3.88	4.22	82.3
			2.0	4.20	4.28	82.2
			3.0	4.58	4.50	81.5
			4.0	4.98	4.68	81.2
			5.0	4.80	4.57	81.5
			6.0	4.98	4.69	81.1
9 (74.9)	Hung and Lutes (1987)	3, 8	0.5	3.73	4.70	79.3
			1	5.43	5.39	78.0
			1.5	6.23	5.68	77.3
			2	7.50	6.34	75.5
			2.5	8.03	6.55	74.7
			3	7.03	6.17	75.8
			3.5	8.47	6.64	74.8
			4	8.87	6.84	74.3
10 (128)	Hung et al. (1993)	3, 8	2.0	5.18	5.23	78.4
			2.5	6.18	5.53	78.1
			3.0	6.53	5.79	77.1
			3.5	6.85	5.99	76.2
11 (252)	Lee et al. (2016)	3, 10	0.2	9.01	6.82	74.8
			0.4	10.29	7.28	73.6
			0.8	10.84	7.54	72.9
			1.6	11.82	7.95	72.2
12 (693)	Lee et al. (2015)	3, 4	0.4	6.60	6.34	74.6
			0.8	8.20	6.92	73.2
			1.2	10.10	7.66	71.7
			1.6	8.67	7.22	72.3
			2.0	10.60	7.85	71.1

FBW = final body weight.
[1] The average final body weight of fish in all tanks when the growth trial ended.
[2] The number of tanks assigned to each feeding rate.
[3] An individual value in each column is represented as the average of replicates corresponding to the respective feeding rate.
[4] Body energy content was calculated using the following values: crude protein 23.6 kJ/g, crude lipid 39.3 kJ/g, and nitrogen free extract (NFE) 17.7 kJ/g (Deng et al., 2003).

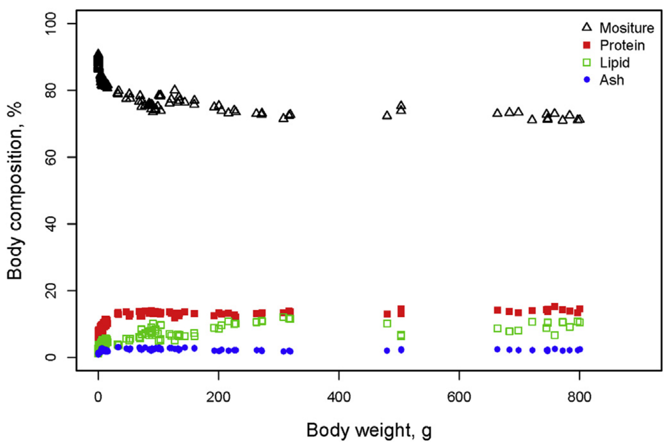

Fig. 1. Plots of body compositions (%; as wet basis) including moisture, protein, lipid, and ash obtained from published studies (Hung and Lutes, 1987; Hung et al., 1993; Deng et al., 2003; De Riu et al., 2012; Lee et al., 2015; Lee et al., 2016) on white sturgeon fed at various feeding rates (% body weight per day).

proportion of feed loss is not proportional to FR and the use of FCR would have provided biased results. The statistical relationships between the body composition (lipid, moisture) or energy and the FR were also investigated by the logistic curve except the moisture. Polynomial regression models of different orders were investigated for moisture due to the data behavior of the moisture and FR pair. Then the estimates of SGR, lipid, moisture and energy were obtained at different proportions of OFR. Since the main goal of the current study is to establish the behavior of the growth, lipid, body energy and moisture when white sturgeon are fed at different proportions of OFR, a nonparametric curve fitting approach was utilized to obtain the growth, body composition, and body energy curves under different proportions of OFR across body weights. The estimated SGR, lipid, energy and moisture were utilized as a response to establish functional relationships with the body weight using nonparametric approach for visualization rather than model development.

The sections below describe the logistic model and estimation of OFR (Section 2.2.1), the development of statistical relationships between lipid, energy, and moisture vs. FR (Section 2.2.2), the computation of SGR, lipid, energy, and moisture at various FR as a proportion of OFR (Section 2.2.3), the nonparametric curve fitting procedures (Section 2.2.4), and the determination of differences of 100% OFR with various proportions of OFR (Section 2.2.5).

2.2.1. Logistic curve model and method to estimate OFR for objectives one and two

The logistic curve was used to develop the statistical relationship between SGR (response) and FR (predictor) for all datasets in objectives 1 and 2. After this relationship was established, OFR was determined using an iterative approach where the stopping criteria depended on how rapidly SGR approached an asymptote.

2.2.1.1. Logistic curve model. A logistic curve model is a sigmoidal function, being frequently used to model biological processes where the response is typically increasing at an increasing rate and then increasing at a decreasing rate then leveling off after a certain point (Morgan et al., 1975; Bates and Watts, 1988). This model has the form,

$$y = m(x, \boldsymbol{\theta}) + \varepsilon = \frac{\theta_1}{1 + \exp[-(\theta_2 + \theta_3 x)]} + \varepsilon \tag{1}$$

where y is the response (SGR), $m(x, \boldsymbol{\theta})$ is the mean function which depends on the vector valued parameter $\boldsymbol{\theta} = \theta_1, \theta_2, \theta_3$, and a vector predictor x (FR). Logistic curve fitting used the nonlinear least squares (nls) function in the statistical software R (R Core Team, 2015). The nls function was used to estimate $\boldsymbol{\theta}$, as the values that minimize the residual sum of squares. Due to the nonlinear nature of $m(x, \boldsymbol{\theta})$, the minimization process was done by an iterative method (such as Newton–Raphson, Gauss-Newton; see Bates and Watts, 1988 for other iterative algorithms), which requires an appropriate initial values. The R function SSlogis, which is a self-starting function, can avoid the step of identifying initial values (Sec. 8.1.2; Pinheiro and Bates, 2000). To use the function SSlogis in R, re-parametrization of Eq. 1 was required as shown below

$$m(x, \boldsymbol{\theta}) = \frac{\varnothing_1}{1 + \exp\left[\frac{-(x - \varnothing_2)}{\varnothing_3}\right]} \tag{2}$$

where ($\varnothing_1$, $\varnothing_2$, $\varnothing_3$)= ($\theta_1, -\theta_2/\theta_3,\ 1/\theta_3$). Note that as x approaches positive infinity, $m(x,\ \boldsymbol{\theta})$ approaches $\varnothing_1$ and when x approaches negative infinity, $m(x,\ \boldsymbol{\theta})$ approaches 0.

The residual analyses on the logistic curve fitting for the 19 datasets (objective 1) and the 12 datasets (objective 2) were done based on the residual assumptions for the nonlinear regression. Regarding the normality of the residuals, the Shapiro–Wilk normality test was applied to the logistic regression fits and, except the fits for datasets 7 and 19 (objective 1), the rest of them had $P > 0.05$, suggesting the normality of the residuals. Datasets 7 and 19 (objective 1) had the P-value fairly close to 0.05 (i.e., 0.03). In addition, assumption of variance homogeneity was evaluated using the Levene's test (Ritz and Streibig, 2008). All datasets except the dataset 19 (objective 1) having the P-value of 0.0406 were met the assumption ($P > 0.05$). Dataset 19 (objective 1) was still included in the analysis because this probability was sufficiently close to 0.05. Based on the Ljung–Box test (Ljung and Box, 1978), all residuals of the logistic curve fits for the 19 datasets (objective 1) and the 12 datasets (objective 2) were not correlated.

2.2.1.2. Estimation of OFR. After fitting the logistic curve to the given datasets (19 datasets for objective 1 and 12 datasets for objective 2), an OFR was estimated for each dataset. To estimate an OFR, an iterative approach was used as follows. Assume that for data j, the FR lies in the interval (FR_{min}, FR_{max}). Now consider the partition of that interval into n subintervals, i.e., $(FR_{min}, FR_{max}) = \cup_{i=1}^{n}(FR_{i-1}, FR_i)$. Further assume that we have the logistic curve fit $\widehat{g}(\cdot)$, where it is estimated from the data j. The intuitive way of choosing an OFR is to pick a FR where the next choice of FR will not contribute that much in the accumulation of the SGR. In other words, one can pick a stopping criterion $\xi > 0$, for which the OFR is the first FR_i satisfying

$$\left|\frac{\widehat{g}(FR_{i+1}) - \widehat{g}(FR_i)}{FR_{i+1} - FR_i}\right| < \xi \tag{3}$$

This is an approximation to find the maximum of the function $\widehat{g}$, and by allowing the stopping criteria parameter ξ to be positive (not zero) we can estimate the FR value where the SGR levels off. As it is obvious from above, small ξ values will result in estimates that are more conservative while large values may result in a more liberal estimation of OFR. The selection of ξ for each dataset is unique which differs from taking a fixed percentage of the asymptote. The ξ used for each data set was equal to the range of the SGR for a given weight class times 0.05. Essentially, this normalizes all datasets through Eq. 3 such that ξ is selected based on a proportion of the range of the response, which is unique for each dataset. In a more mathematical sense, this stopping criteria searches for the point where the rate of change (or the slope) in the response is small enough, i.e., the rate of change does not change that much. In a biological sense, we seek for the FR that even if the fish is fed beyond that FR, the contribution to SGR is not significant. Here the meaning of significant (i.e., ξ) is defined by the user, this is a very commonly used stopping criteria in most of the iterative algorithms which are structured for optimization (Berinde, 1997).

2.2.2. Developing statistical relationships between body lipid, energy, and moisture (response) vs. feeding rate (predictor)

The statistical relationship between SGR and FR was established in objective 1 as part of the process of determining OFR (see Section 2.2.1). The relationship between lipid or energy and FR was developed using the same approach as described in Section 2.2.1 using Eqs. 1 and 2 except now the response was energy or lipid and the predictor FR. Polynomial regression models were used for moisture because the relationship between moisture and FR did not fit a logistic curve. A different approach was used to investigate the relationship between the various FR and corresponding body moisture content in each of the 12 datasets because body moisture content linearly or non-linearly decreased with increasing FR, suggesting that the logistic curve fitting would not be the best fit. Instead, we tested a polynomial regression model of order from 1 to 6 for each of the 12 datasets where moisture was the response variable and FR was the independent variable. Then, the best-fit model, based on the smallest Akaike information criterion (AIC) value for each dataset, was selected.

The assumption of variance homogeneity, and independence and normality of residuals (as described in Section 2.2.1.1) was tested and confirmed for all models.

2.2.3. Computation of SGR (objective one) and body lipid, energy, and moisture (objective two) at various feeding rates

Once the statistical relationships are established for SGR vs. FR (objective 1, Section 2.2.1.1) and lipid, energy, and moisture vs. FR (objective 2, Section 2.2.2), then we have a predictor or $\widehat{g}(\cdot)$ for a given variable vs. FR. We can now estimate $\widehat{g}(\cdot)$ for the OFR determined from Section 2.2.1.2 (or proportions of OFR) for the 19 (objective 1) or 12 (objective 2) datasets as follows

$$\widehat{y}_{rOFR} = \widehat{g}_y(r \times OFR) \tag{4}$$

where $\widehat{y}_{rOFR}$ was the response of either SGR, lipid, energy, or moisture, and $\widehat{g}_y(\cdot)$ was the logistic curve (polynomial for moisture dataset) fit specific to the given dataset and r was proportion of the estimated OFR for the given dataset (i.e., $r = 0.3,\ 0.5,\ 0.7,\ 0.9,\ 1.0,$ and 1.1, OFR were 30%, 50%, 70%, 90%, 100%, and 110%, respectively). Essentially, a response is estimated for every dataset for a given proportion of OFR. For example, 19 SGR values were estimated for a given r in objective 1. Similarly, 12 lipid, energy or moisture values were estimated for a given r for objective 2.

2.2.4. Nonparametric curve fitting (objectives one and two)

The main goal of the current study is to establish the behavior of SGR, lipid, energy and moisture when white sturgeon are fed at various proportions of OFR. Hence, once the 19 estimated SGR and 12 estimated lipid, energy and moisture contents at different OFR levels were determined from Section 2.2.3, a nonparametric (spline smoothing) technique was used to create curves to make appropriate visual comparisons at different body weights.

A spline function is a curve constructed from polynomial segments that are subject to conditions or continuity at their joints. In statistics, smoothing splines (which are constructed from spline functions) have been used in fitting curves to data without assuming any parametric form (Ahlberg et al., 1967). Assume that $(x_i, y_i)_{i=1}^{n}$ is a sequence of observations modeled by relation $y_i = g(x_i)$, where y represents the response variable (SGR, lipid, energy or moisture) and x represents body weight. The smoothing spline estimate $\widehat{g}$ of the function g is defined to be the minimizer (over the class of twice differentiable functions) of

$$\sum_{i=1}^{n} (y_i - \widehat{g}(x_i))^2 + \lambda \int \left[\widehat{g}''(t)\right]^2 dt \tag{5}$$

where the first part is the regular sum of residuals, and the second part is the penalty term which accounts for the bias-variance trade-off. Note that the penalty term is controlled by the tuning parameter λ. As $\lambda \to 0$ the smoothing spline converges to interpolating spline or fitting every data point making the model over parameterized, and as $\lambda \to \infty$ the roughness penalty becomes paramount and the estimate converges to a linear least squares estimate or ordinary least squares making the model a simple regression. Therefore, it is crucial to pick optimal tuning parameter λ to avoid over/under-fitting. The tuning parameter can be chosen via Cross-Validation (CV), based on minimizing the sum of one-leave-out squared prediction errors, or one can utilize m-fold CV, which involves dividing the sample into m subsamples, leaving each out iteratively. This technique is called Generalized Cross-validation (GCV) and it is a faster simplified version of CV. One needs to beware of over smoothing (small variance, large bias) and of under smoothing (large variance, small bias), where the latter is also known as under fitting. The tuning parameter selection defines the necessary compromise between variance and bias.

2.2.5. Determining differences in estimated curves between various proportions of OFR (objectives one and two)

After the SGR, lipid, energy and moisture (response) vs. body weight (independent) equations were developed at OFR and proportions of OFR (Section 2.2.4), then differences were calculated to better visualize the deviations of the estimated response variables at each proportion of OFR. The deviation was computed, using the formula,

$$d_{y,k} = y_{(k\times 100)\%OFR} - y_{100\%OFR}, \quad k = 0.3, 0.5, 0.7, 0.9, 1.1 \tag{6}$$

where $d_{y,k}$ is the difference between the kth proportion of OFR $(y_{(k\times 100)\%OFR})$ and 100% OFR $(y_{100\%OFR})$ for SGR, lipid, energy, and moisture at different body weights.

3. Results and discussion

3.1. Growth rate models at proportions (0.3 to 1.1) of OFR (objective one)

The logistic curve fits using Eq. 2 for the 19 datasets except the dataset 16 (due to a failure of convergence of the model algorithm) were plotted in Fig. A. The OFR for each of the 19 datasets except the

Table 2
Estimated specific growth rates at proportions (0.3 to 1.1) of optimum feeding rate (OFR; % body weight per day) for 19 datasets.[1]

Dataset (IBW,[2] g)	Estimated 100% OFR[3]	Specific growth rate estimated at each proportion of OFR					
		30%	50%	70%	90%	100%	110%
1 (0.05)	35.9	7.75	10.30	11.82	12.33	12.42	12.47
2 (0.09)	23.1	7.04	9.54	10.56	11.06	11.19	11.28
3 (0.18)	14.4	4.06	6.95	9.17	10.28	10.56	10.73
4 (0.37)	11.6	5.54	8.22	9.05	9.22	9.24	9.25
5 (2.8)	6.8	3.36	5.01	6.34	7.16	7.41	7.58
6 (4.5)	5.8	2.25	4.08	5.48	6.14	6.29	6.38
7 (8.6)	4.9	1.70	3.50	5.04	5.78	5.94	6.03
8 (10.0)	4.8	1.45	2.98	4.41	5.19	5.38	5.49
9 (27.9)	3.8	0.98	2.10	2.64	2.77	2.79	2.80
10 (37.0)	3.0	0.96	1.86	2.27	2.38	2.39	2.40
11 (49.0)	2.5	0.63	1.40	1.78	1.87	1.88	1.88
12 (61.9)	2.4	0.79	1.30	1.43	1.44	1.44	1.45
13 (30.5)	3.4	0.82	1.78	2.47	2.73	2.77	2.79
(360)	1.8	0.36	0.92	1.38	1.55	1.58	1.59
15 (419)	1.6	0.42	0.72	0.91	0.99	1.01	1.02
16 (470)		N/A[4]					
17 (544)	1.5	0.71	0.95	0.96	0.96	0.96	0.96
18 (617)	1.5	0.60	0.86	0.90	0.90	0.90	0.90
19 (764)	1.4	0.23	0.47	0.64	0.70	0.71	0.71

IBW = initial body weight.
[1] Note: 100% OFR is identical to the proportion 1 of OFR.
[2] The average initial body weight of fish in all tanks when the growth trial began.
[3] Estimated 100% OFR was calculated by the iterative approach applied to the logistic curve fit using Eq. 3.
[4] Not applicable due to failure of convergence of the tested model algorithm.

dataset 16, estimated by the logistic curve model is shown in Table 2. Estimated SGR at the different proportions (0.3, 0.5, 0.7, 0.9, 1.0, 1.1) of OFR for the 19 datasets, except the dataset 16, are presented in Table 2 and Fig. 2. Curve fitting the estimated SGR at each of the different proportions of OFR against body weights varying from 0.05 to 800 g using the spline-smoothing function (Eq. 5) is presented in Fig. 3A. In general, there is a significant change in the estimated SGR when the body weight of white sturgeon is small (less than 60 g), and the estimated SGR continuously decrease but the rate of change gets smaller as body weight increases. For example, the estimated SGR of white sturgeon when fed at 100% OFR dramatically drops from 12.4% to 1.4% when the initial body weight increases from 0.05 (first exogenous feeding) to about 60 g. On the other hand, the estimated SGR of white sturgeon fed at the same FR shows little change in the estimate from 1.4% to 0.7% when the initial body weight increases from about 60 to 764 g. Dumas et al. (2010) suggest using the thermal-unit growth coefficient (TGC) instead of SGR for modeling fish growth. In the current analyses, SGR was not used to estimate growth of sturgeon making current analyses different than estimating body weight change over time with fish, which was a criticism of using SGR in the Dumas paper. The TGC was calculated (in Table A) and compared with SGR in the current study, the correlation between TGC and SGR for the 19 datasets was over 0.992 for 17 datasets, and dataset 1 and 12 had correlations of 0.965 and 0.988, respectively. Although temperature can be important in evaluating growth of fish, our analyses show that there is a very high correlation between SGR and TGC in the 19 datasets. Furthermore, we were not using SGR as a coefficient in an exponential growth model, which would have been incorrect.

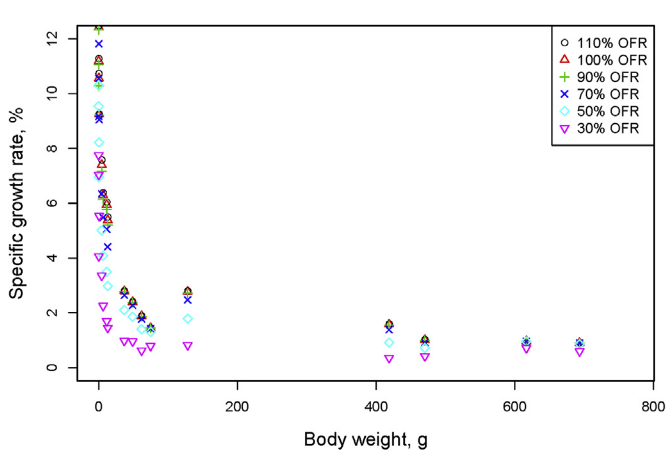

Fig. 2. Specific growth rates (%) at the different proportions (0.3, 0.5, 0.7, 0.9, 1.0, 1.1) of optimum feeding rate (OFR; % body weight per day) for the 19 datasets except the dataset 16 (initial body weight = 470 g), estimated by the logistic curve model are presented.

The previously developed prototype feeding and growth models for white sturgeon (Cui and Hung, 1995) have been applied in farmed and experimental situations because the prototype models can provide a guidance/standard for evaluating feeding rate-dependent growth performance. However, the approach in determining OFR in the current study differs from the approach used in prototype models. First, an iterative approach was used in the current study to select OFR as the FR at which the growth was maximal or approached maximal. On the other hand, analysis of variance (ANOVA) and multiple range tests were used to determine the minimum FR which produced growth not significantly different from that of fish fed at the highest rate (Cui and Hung, 1995) which is different compared with the technique used in the current study to determine OFR. It is noteworthy that use of the ANOVA and multiple range tests which reflect growth response to FR is discrete and these approaches are not appropriate to determine optimum levels because the dose–response relationship between FR and growth is continuous (see a critical review by Shearer, 2000; Lee et al., 2014). Second, our SGR models show how the growth rate changes in white sturgeon weighing to 0.05 g (average body size when first exogenous feeding starts), whereas the prototype growth model is limited to 50 g (Cui and Hung, 1995). Taken together, the SGR models developed here can be more useful in establishing functional relationships with body weight for various proportions of OFR. On the other hand, it needs to be emphasized that the prototype growth model can provide estimations at a wide range of temperatures from 10 to 26 °C (Cui and Hung, 1995), whereas our SGR models curves in the current study are appropriate from 18 to 20 °C.

There are many factors affecting growth of fish, including abiotic factors (e.g., temperature, light, oxygen) and biotic factors (e.g., nutrient compositions of diet, genetic strains, fish size) (Brett, 1979). Therefore, the SGR results can be applied within a relatively narrow range of conditions. However, the conditions used for the current study are comparable to those practically applied in a commercial scale in terms of genetic strains, temperature, and feeds due to the geographic proximity between the site in which majority of the growth trials was conducted and the location of commercial farms (within about 80 km) located in Sacramento, California, USA. The majority of production for sturgeon aquaculture in the USA comes from white sturgeon, 95% from the California producers (F.S. Conte, University of California, Davis, CA, USA; personal communication). In addition, the feeding rate optimal for maximum growth of fish can be changed for a given rearing condition. Especially, diet quality such as gross energy, nutrient composition, and digestibility are important factors affecting OFR. Thus, examining the patterns of proportions of optimum dietary gross energy can be used to evaluate the overall feeding program for white sturgeon and can be of interest for future research. Similarly, description of changes in whole-body nutrient

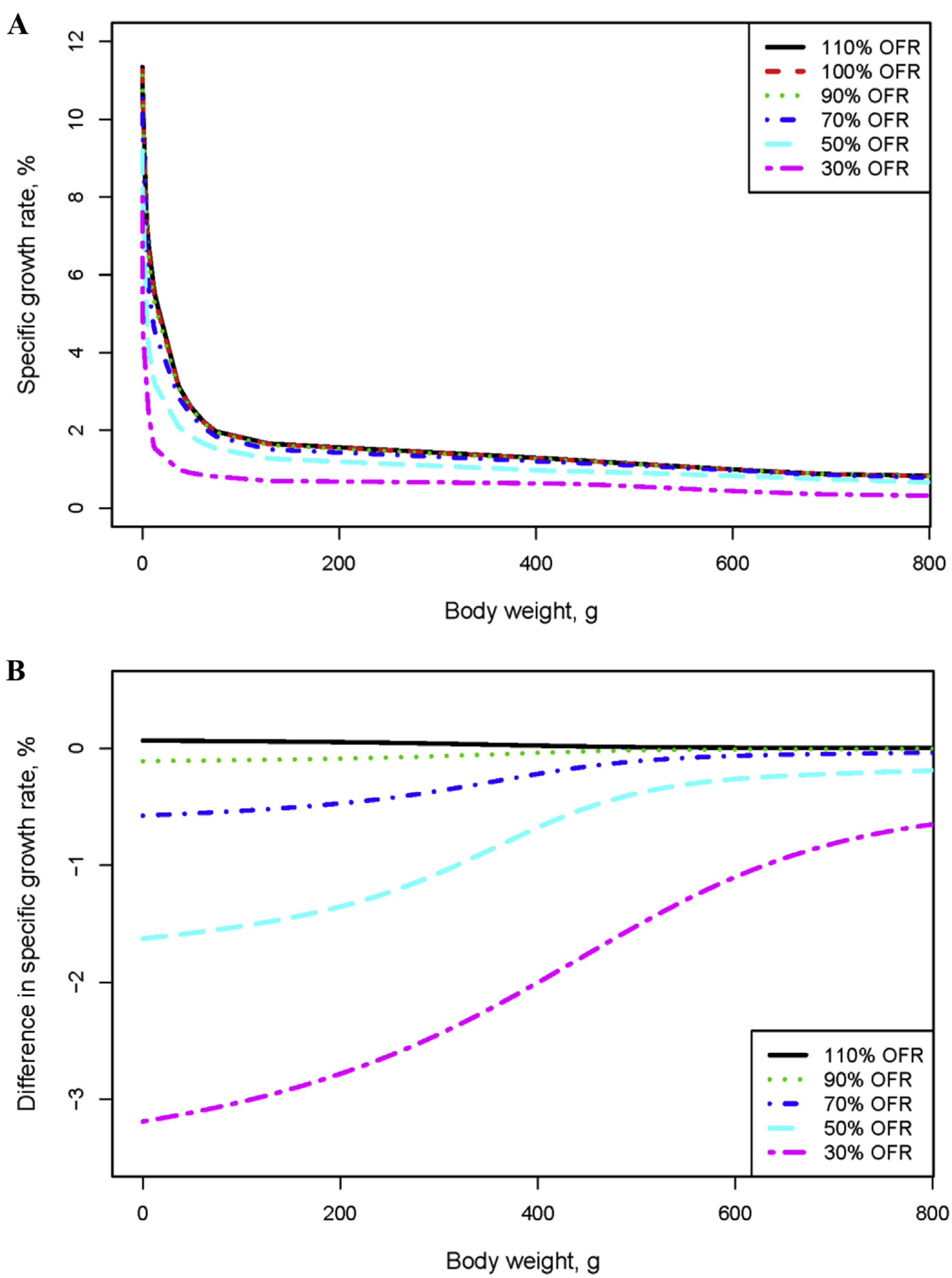

Fig. 3. Specific growth rate curves for different proportions (0.3, 0.5, 0.7, 0.9, 1.0, 1.1) of optimum feeding rate (OFR; % body weight per day) developed using the spline-smoothing function (Eq. 5) (A). Also, differences (B) in specific growth rate curves at any proportion of OFR from specific growth rate at 100% OFR (i.e., 30 vs. 100%; 50 vs. 100%; 70 vs. 100%; 90 vs. 100%; 110 vs. 100%). Note that 100% OFR is equivalent to the proportion 1 of OFR.

compositions and energy of white sturgeon when fed at different proportions of an optimum dietary gross energy as presented in the current study will be worth further study.

A previous study (Cui et al., 1997) showed that white sturgeon achieved the best growth when they were fed continuously for 24 h per day using an automatic feeder (model-100, Double A Brand Co., Dallas, TX, USA). This precluded us from using the traditional approach of feeding to apparent satiation that is commonly used when studying the relationship between FR and growth and body composition (Dumas et al., 2007). We found that using various FR as percent body weight per day to establish the OFR for a fixed period is more informative. With the established OFR we can use the different proportions of OFR to establish its relationship with growth under different FR. The Fig. 3B shows as body weight increases the difference between feeding fish feed at various proportions of OFR and 100% OFR decreases. This trend emphasizes the importance of feeding fish optimally when they are young.

3.2. Development of body lipid, energy, and moisture models at proportions (0.3 to 1.1) of OFR (objective two)

The statistical relationship between the response variable (lipid) and the predictor variable (various FR) for the 12 datasets was investigated through testing the logistic curve model (Eq. 2), and the logistic curve fitting for each of the 12 datasets is shown in Fig. B. The OFR for each of the 12 datasets estimated by the logistic curve model is shown in Table 3. Body lipid content at the different proportions (0.3, 0.5, 0.7, 0.9, 1.0, and 1.1) of OFR for the 12 datasets, estimated by the logistic curve model is presented in Table 3. Curve fitting the estimated body lipid content at each of the different proportions of OFR against body weights varying from 0.1 to 700 g using the spline-smoothing function is presented in Fig. 4A. Differences in the lipid curves at a given proportion of OFR from those at 100% OFR (i.e., 30% vs. 100% OFR; 50% vs. 100%; 70% vs. 100%; 90% vs. 100%; 110% vs. 100%) are plotted in Fig. 4B. A pattern of changes in estimated body lipid content at all proportions of OFR reflects a sigmoid curve, showing continuous increase in lipid content with increasing body weight up to about 550 g, then start to level off afterwards. As body weight increases, the calculated difference in the body lipid content at any given proportion of OFR from that at 100% OFR gets smaller while body weight increases, then remains constant when body weight becomes larger than about 550 g (Fig. 4B). This trend might be attributed to body lipid changes, which might become less responsive to various FR as body weight increase. On the other hand, regardless of FR a continuous increase in body lipid content as white sturgeon grow indicates that lipid deposition is a major

Table 3
Estimates of body lipid (%), moisture (%), and energy (kJ/g) as wet basis at proportions (0.3 to 1.1) of optimum feeding rates (OFR; % body weight per day) calculated using Eq. 4 for body lipid, moisture, and energy, respectively.[1]

Dataset (FBW,[2] g)	Estimated 100% OFR[3]	Variable	Body lipid, energy, and moisture content calculated at each proportion of OFR					
			30%	50%	70%	90%	100%	110%
1 (0.10)	35.9	Lipid	1.55	1.69	1.79	1.86	1.89	1.91
		Energy	2.33	2.43	2.50	2.56	2.58	2.59
		Moisture	89.91	89.64	89.41	89.22	89.14	89.08
2 (0.20)	23.1	Lipid	1.69	2.06	2.27	2.36	2.39	2.40
		Energy	2.36	2.55	2.65	2.70	2.72	2.73
		Moisture	89.92	89.40	89.19	89.01	88.92	88.84
3 (0.31)	14.4	Lipid	1.45	1.66	1.89	2.15	2.29	2.44
		Energy	2.30	2.46	2.60	2.70	2.75	2.79
		Moisture	89.79	89.22	88.96	88.73	88.54	88.24
4 (0.65)	11.6	Lipid	2.32	2.70	2.96	3.13	3.19	3.23
		Energy	2.74	3.03	3.19	3.28	3.31	3.32
		Moisture	88.43	87.36	86.85	86.67	86.63	86.59
5 (4.5)	6.8	Lipid	2.88	3.56	3.99	4.23	4.30	4.34
		Energy	3.52	3.74	3.89	3.99	4.03	4.06
		Moisture	84.70	84.45	84.19	83.94	83.81	83.69
6 (6.4)	5.8	Lipid	3.86	4.37	4.70	4.90	4.96	5.01
		Energy	3.93	4.08	4.18	4.24	4.26	4.28
		Moisture	82.87	82.75	82.62	82.49	82.43	82.37
7 (11.6)	4.9	Lipid	4.36	4.77	5.06	5.25	5.32	5.38
		Energy	4.25	4.42	4.56	4.67	4.72	4.76
		Moisture	82.58	82.17	81.84	81.58	81.48	81.41
8 (13.1)	4.8	Lipid	4.05	4.43	4.68	4.84	4.89	4.93
		Energy	4.27	4.42	4.52	4.60	4.63	4.65
		Moisture	82.48	81.95	81.33	81.28	81.41	81.50
9 (74.9)	1.9	Lipid	4.07	5.09	6.02	6.78	7.09	7.36
		Energy	4.81	5.29	5.68	5.98	6.11	6.21
		Moisture	78.59	77.92	77.84	76.52	75.73	75.12
10 (128)	3.4	Lipid	2.22	4.35	5.96	6.64	6.78	6.86
		Energy	4.47	5.01	5.46	5.81	5.95	6.07
		Moisture	80.08	79.04	78.00	76.96	76.44	75.92
11 (252)	1.6	Lipid	10.21	10.94	11.36	11.59	11.66	11.71
		Energy	7.27	7.56	7.75	7.86	7.90	7.93
		Moisture	73.28	72.89	73.09	73.03	72.64	71.86
12 (693)	1.5	Lipid	7.91	8.41	8.89	9.34	9.56	9.77
		Energy	6.76	7.02	7.23	7.42	7.50	7.58
		Moisture	73.63	73.16	72.68	72.20	71.96	71.72

FBW = final body weight.
[1] Note: 100% OFR is identical to the proportion 1 of OFR using Eq. 3.
[2] The average final body weight of fish in all tanks when the growth trial ended.
[3] Estimated 100% OFR from Eq. 3 and the proportions of OFR from Eq. 4.

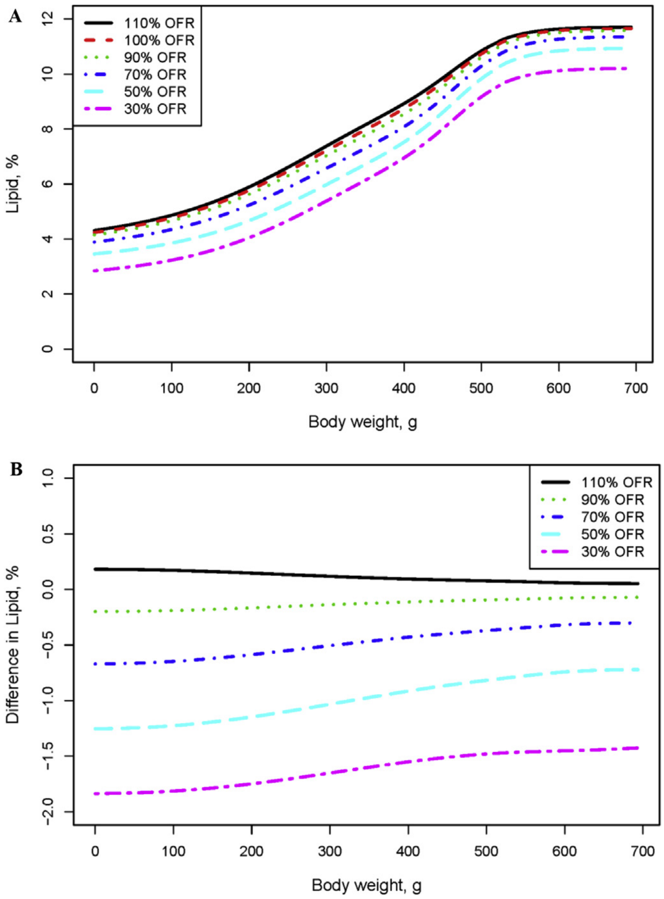

Fig. 4. Estimated body lipid curves as wet basis (A) at proportions (0.3 to 1.1) of optimum feeding rate (OFR; % body weight per day) and difference (B) in estimated body lipid curves at any proportion of OFR from the estimated body lipid curve at 100% OFR (i.e., 30% vs. 100% OFR; 50% vs. 100%; 70% vs. 100%; 90% vs. 100%; 110% vs. 100%). Note that 100% OFR is equivalent to the proportion 1 of OFR.

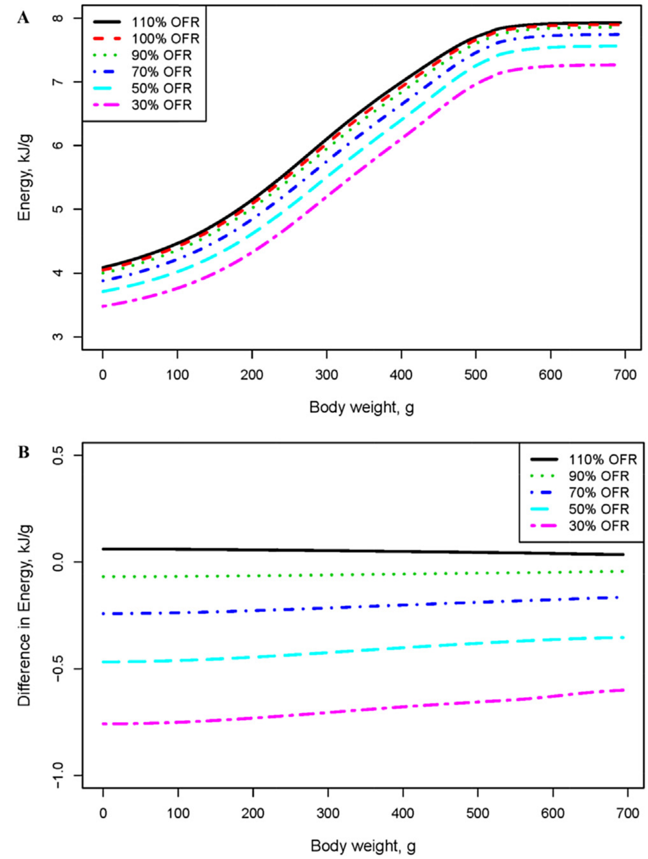

Fig. 5. Estimated body energy curves as wet basis (A) at proportions (0.3 to 1.1) of optimum feeding rate (OFR; % body weight per day) and difference (B) in estimated body lipid curves at any proportion of OFR from the estimated body lipid curve at 100% OFR (i.e., 30% vs. 100% OFR; 60% vs. 100%; 70% vs. 100%; 80% vs. 100%; 90% vs. 100%; 100% vs. 100%; 110% vs. 100%). Note that 100% OFR is equivalent to the proportion 1 of OFR.

contributor to gain in body mass of white sturgeon up to about 550 g. This may reflect that white sturgeon at early developmental stages (e.g., juvenile, yearling) requires a high lipid level in diets, supported by findings from Hung et al. (1997) showing that white sturgeon (110 g) displayed good growth without any adverse effects on body composition and liver lipogenic enzyme activities from feeding on diets with high lipid content (25.8 to 35.7 g/100 g diet). The proportional increase of OFR with increased body lipid observed in white sturgeon in the current study is a common phenomenon across animal species. However, this increase of body lipid with increasing FR in white sturgeon larvae right after hatch suggests that dietary lipid is a very critical nutrient to the early development of white sturgeon.

Overall procedures to describe the relationship between body energy and various FR tested in each of the 12 datasets were similar to those described above for body lipid. Through testing the logistic curve model, the logistic curve fitting for each of the 12 datasets is shown in Fig. C. Body energy content at the different proportions (0.3, 0.5, 0.7, 0.9, 1.0, and 1.1) of OFR for the 12 datasets, estimated by the logistic curve model is presented in Table 3. Curve fitting the estimated body energy content at each of the different proportions of OFR against body weights varying from 0.1 to 700 g using the spline-smoothing function is presented in Fig. 5A. Differences in the estimated energy curves at a given proportion of OFR from those at 100% OFR (i.e., 30% vs. 100%; 50% vs. 100%; 70% vs. 100%; 90% vs. 100%; 110% vs. 100%) are plotted in Fig. 5B. A pattern of changes in the calculated differences of body energy estimates between different OFR levels as body weight increases is similar to those of body lipid.

Unlike body lipid and energy content, the relationship between body moisture and various FR tested in each of the 12 datasets was investigated through testing polynomial regression models of order from 1 to 6 and selecting the best-fit model based on the model selection criterion (AIC). The chosen polynomial regression fits to the 12 datasets are presented in Fig. 4A. Body moisture content at the different proportions (0.3, 0.5, 0.7, 0.9, 1.0, and 1.1) of OFR for the 12 datasets, estimated by the chosen polynomial regression model is presented in Table 3. Curve fitting the estimated body moisture content at each of the different proportions of OFR against body weights varying from 0.1 to 700 g using the spline-smoothing function is presented in Fig. 6A. The body moisture curves show an inverse trend compared with those of body lipid content as shown in Fig. 4A. This can be explained by the homeostasis of cell size to maintain cell functionality through replacement of moisture with organic matter such as lipid (McCue, 2010). Differences in the estimated moisture curves at a given proportion of OFR from those at 100% OFR (i.e., 30% vs. 100%; 50% vs. 100%; 70% vs. 100%; 90% vs. 100%; 110% vs. 100%) are plotted in Fig. 6B. The calculated difference in the body moisture content at any given proportion of OFR from that at 100% OFR gets dramatically larger when body weight increases from 0.05 g to

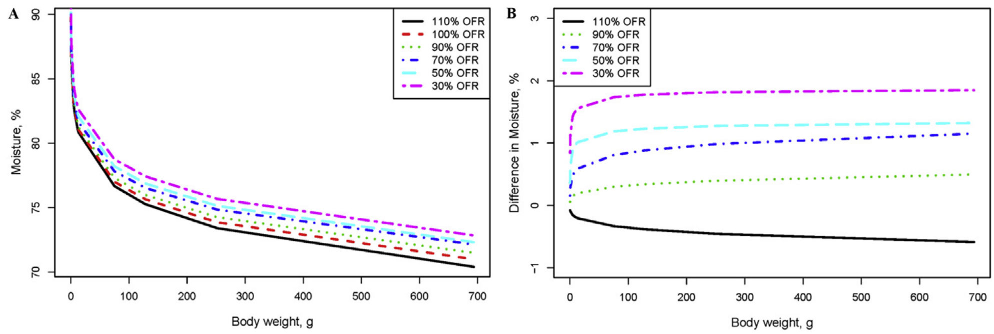

Fig. 6. Estimated body moisture curves (A) at proportions (0.3 to 1.1) of optimum feeding rate (OFR; % body weight per day) and difference (B) in estimated body lipid curves at any proportion of OFR from the estimated body lipid curve at 100% OFR (i.e., 30% vs. 100% OFR; 60% vs. 100%; 70% vs. 100%; 80% vs. 100%; 90% vs. 100%; 100% vs. 100%; 110% vs. 100%). Note that 100% OFR is equivalent to the proportion 1 of OFR.

about 50 g, then remain relatively constant when body weight becomes larger than about 100 g (Fig. 6B).

White sturgeon, known as living fossils (Gardiner, 1984), are thought to have a similar pattern of changes in whole-body nutrient compositions (%) as fish grow in comparison to that of modern teleost such as salmonids (Shearer, 1994; Dumas et al., 2007; Lee et al., 2016). An overall pattern of changes in the compositions of white sturgeon (current study) and rainbow trout (*Oncorhynchus mykiss*; Dumas et al., 2007) shows that body moisture rapidly decreases, whereas body protein and lipid dramatically increases while they are very young and small. Then, these variables remain rather constant as body size increases. On the other hand, levels of body ash of the two species seem to persist throughout their life cycles. A previous study using extensive datasets (over 500 sets of observations) from 66 studies to investigate the relationships between body weight and rates of nutrient deposition in rainbow trout produced growth rate (gram per day) prediction models as function of body compositions as well as an individual nutrient deposition model for each body composition as function of body weight (Dumas et al., 2007). These models can predict reliable estimates of body composition and conversion of nutrients to biomass that help describe growth process in a wide range of conditions (e.g., genetic strains, feed composition, environment) because of the extensive survey on literature (Dumas et al., 2007). Both body protein and ash of white sturgeon fed at different FR at different initial body weights in the current study remain quite constant. This is different from those reported by Shearer (1994) that body protein and ash are life cycle and size-dependent in salmonids. In addition, others (Dumas et al., 2007) found that body protein was a key predictor of body weight across life stages, whereas in the current study protein was relatively constant across body weights. The difference between studies is likely that the life span of salmonids is so much shorter than sturgeon. Data collected from the current study were during the first year (from first exogenous feeding at 0.05 g to about one-year-old at 800 g) of a long-lived species whereas those from salmonid (Shearer, 1994; Dumas et al., 2007) were throughout the whole life cycle.

Because the purpose of developing our models was focused on SGR, body lipid, energy and moisture responses when white sturgeon are fed at various feeding levels (i.e., proportions of OFR), selection of datasets was limited to the studies conducted for investigating the effects of feeding rate on growth performance and body lipid, energy and moisture changes. Some datasets used in the current study was relatively small compared with that from Dumas et al. (2007). However, most studies that produce the datasets used in the current study were conducted under similar conditions such as experimental set-ups (i.e., all growth trials were performed in the same facility, Center for Aquatic Biology and Aquaculture in University of California at Davis, USA) and rearing practice carried out by the same laboratory. This suggests that the inter-study variability of the datasets used for the current study is small; however, the conditions for application of our models may be restricted to the given conditions described in the FR studies (see Table A). Nonetheless, the diets (either commercial or formulated) used in the aforementioned feeding rate studies that provided the datasets for developing our new models were appropriately selected to meet the nutrient requirements for the given developmental stage of sturgeon (see Table A). Many of the diets that were used in the studies are commercial feeds that have been used on white sturgeon farms in California, USA. This clearly suggests that the interpretation of these results are applicable to conditions in which researchers and farmers use similar diets.

4. Conclusion

Specific growth rate as well as body lipid, energy, and moisture descriptions developed from the current study can provide reliable information for white sturgeon ranging from 0.05 g (first-feeding) to about 800 g when fed at various feeding levels (i.e., 30% to 110% of optimum feeding rate). To our knowledge, these are the first description of changes in nutrient compositions when white sturgeon are fed at various feeding rates across a range of body weights varying from 0.1 to 700 g, and a similar work to ours has not been performed in other fishes. Finally, due to the distinctive biology of white sturgeon as mentioned earlier, the nature of the data collected, and the unique nonparametric modeling technique we used in the current study, the relationships we established between the FR and growth, body energy, lipid, and moisture are more suitable to sturgeon aquaculturists. Ideally, information from this study will help design future experiments by examining conditions where there are large differences or rapid changes in SGR, body lipid, energy or moisture. Future optimization models require this type of data to be of practical value to the producer. Furthermore, data of this type can be collected in controlled experimental settings and validated with field data from commercial sturgeon operations.

Acknowledgments

This work was supported by the Department of Animal Science, College of Agriculture and Environmental Science, and the California Agricultural Experiment Station of the University of California-Davis.

Appendix

Table A
List of the 19 datasets obtained from the 6 published studies used for describing change of growth rate when white sturgeon are fed at various feeding rates (adopted and modified from Table 1 of Lee et al., 2014).

Dataset number	Source	IBW,[1] g; FBW,[2] g	Number of replications,[3] Duration of feeding, week	FR, % BW per day	SGR,[4] % BW increase per day (TGC,[5] $g^{1/3}/(°C \cdot d)$)	IE,[6] kJ	CP,[7] %	CL,[8] %	Temperature[9] °C
1	Deng et al. (2003)	0.05; 0.10	4, 1	10, 20, 30, 40, 50, 60	7.5, 9.9, 11.0, 11.2, 11.1, 11.7 (0.53, 0.68, 0.80, 0.80, 0.80, 0.82)	19.1	52.5	10.3	19.2
2	Deng et al. (2003)	0.09; 0.20	4, 1	5, 10, 15, 20, 25, 30	5.3, 9.6, 11.5, 12.1, 12.1, 13.0 (0.50, 0.92, 1.10, 1.15, 1.17, 1.23)	19.1	52.5	10.3	19.3
3	Deng et al. (2003)	0.18; 0.31	4, 1	2.5, 5.0, 7.5, 10.0, 12.5, 15.0	2.0, 5.5, 6.8, 9.2, 10.1, 10.8 (0.20, 0.54, 0.73, 1.01, 1.10, 1.19)	19.1	52.5	10.3	19.3
4	Deng et al. (2003)	0.37; 0.65	4, 1	2.5, 5.0, 7.5, 10.0, 12.5, 15.0	3.9, 7.6, 8.9, 9.2, 8.9, 9.6 (0.51, 1.04, 1.24, 1.28, 1.25, 1.35)	19.3	50.0	12.9	19.0
5	De Riu et al. (2012)	2.8; 4.5	4, 1	3, 4, 5, 6, 7, 8	4.5, 5.8, 6.4, 7.1, 7.6, 7.6 (1.23, 1.63, 1.81, 2.01, 2.17, 2.17)	19.0	48.8	12.3	18.0
6	De Riu et al. (2012)	4.5; 6.4	4, 1	2, 3, 4, 5, 6, 7	2.7, 4.3, 5.2, 6.3, 6.4, 6.2 (0.83, 1.37, 1.68, 2.04, 2.04, 2.05)	19.0	48.8	12.3	18.2
7	De Riu et al. (2012)	8.6; 11.6	4, 1	1, 2, 3, 4, 5, 6	0.9, 2.9, 4.3, 5.5, 6.0, 6.1 (0.34, 1.13, 1.69, 2.25, 2.45, 2.45)	19.0	48.8	12.3	18.0
8	De Riu et al. (2012)	10.0; 13.1	4, 1	1, 2, 3, 4, 5, 6	0.6, 2.6, 3.9, 4.8, 5.6, 5.6 (0.26, 1.06, 1.64, 2.01, 2.34, 2.35)	19.0	48.8	12.3	18.0
9	Hung and Lutes (1987)	27.9; 37.0	3, 2	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.0, 1.0, 1.6, 2.2, 2.5, 2.6, 2.9, 2.8 (0.00, 0.50, 0.82, 1.13, 1.32, 1.371.58, 1.52)	21.2	43.0	16.0	20.2
10	Hung and Lutes (1987)	37.0; 49.0	3, 2	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.5, 1.1, 1.8, 2.3, 2.4, 2.7, 2.2, 2.3 (0.24, 0.59, 1.02, 1.33, 1.40, 1.59, 1.32, 1.42)	21.2	43.0	16.0	20.2
11	Hung and Lutes (1987)	49.0; 61.9	3, 2	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.3, 1.1, 1.5, 2.0, 2.2, 1.9, 1.7, 1.7 (0.16, 0.61, 0.93, 1.26, 1.48, 1.27, 1.10, 1.12)	21.2	43.0	16.0	20.2
12	Hung and Lutes (1987)	61.9; 74.9	3, 2	0.5, 1.0, 1.5, 2.0, 2.5, 3.0, 3.5, 4.0	0.5, 1.1, 1.6, 1.9, 1.6, 1.1, 1.1, 1.4 (0.26, 0.63, 1.03, 1.34, 1.13, 0.81, 0.79, 1.00)	21.2	43.0	16.0	20.2
13	Hung et al. (1993)	30.5; 128	3, 8	2.0, 2.5, 3.0, 3.5	2.2, 2.5, 2.7, 2.8 (1.20, 1.46, 1.59, 1.64)	20.5	40.9	13.8	23.1
14	Lee et al. (2016)	360; 419	3, 2	0.4, 0.8, 1.2, 1.6, 2.0	0, 0.9, 1.2, 1.5, 1.7 (0.06, 1.22, 1.62, 1.99, 2.33)	21.9	41.8	19.0	18.0
15	Lee et al. (2016)	419; 470	3, 2	0.4, 0.8, 1.2, 1.6, 2.0	0.4, 0.7, 1.0, 1.0, 1.0 (0.50, 0.93, 1.46, 1.47, 1.42)	21.9	41.8	19.0	17.9
16	Lee et al. (2016)	470; 544	3, 2	0.4, 0.8, 1.2, 1.6, 2.0	0.6, 1.1, 1.1, 1.2, 1.1 (0.83, 1.63, 1.63, 1.74, 1.65)	21.9	41.8	19.0	18.0
17	Lee et al. (2016)	544; 617	3, 2	0.4, 0.8, 1.2, 1.6, 2.0	0.6, 1.0, 1.0, 1.0, 0.9 (0.82, 1.45, 1.59, 1.56, 1.38)	21.9	41.8	19.0	18.1
18	Lee et al. (2016)	617; 693	3, 2	0.4, 0.8, 1.2, 1.6, 2.0	0.5, 0.9, 0.9, 0.9, 0.9 (0.73, 1.36, 1.46, 1.44, 1.49)	21.9	41.8	19.0	18.3
19	Hung et al. (1995)	764; 1055	3, 8	0.5, 0.9, 1.3, 1.7	0.3, 0.6, 0.8, 0.7 (0.42, 0.81, 1.22, 0.94)	N/A[10]	44.0	15.0	22.4

IBW = initial body weight; FBW = final body weight, FR = feeding rate; SGR = specific growth rate; TGC = thermal-unit growth coefficient; IE = intake energy; CP = crude protein; CL = crude lipid.
[1] The average initial weight of fish in all tanks when the growth trial began.
[2] The average final weight of fish in all tanks when fish were measured or the growth trial ended.
[3] A number of tanks assigned to each feeding rate.
[4] Calculated from the equation: 100 × [ln(FBW) − ln(IBW)]/Days of feeding, where the FBW and IBW were the average final and initial BW. The values in the SGR column represented the average SGR of the replicates corresponding to the respective feeding rate shown in the FR column.
[5] TGC calculated from the equation: $(W_n^{1/3} - W_0^{1/3})/(T \times \text{Days of feeding}) \times 1{,}000$, where the W_n and W_0 were the average final and initial body weights, respectively and T was the average temperature during the feeding trial.
[6] The energy content in the diet as fed was calculated using the following values: crude protein 23.6 kJ/g, crude lipid 39.3 kJ/g, and nitrogen free extract (NFE) 17.7 kJ/g.
[7] Crude protein: % crude protein contained in the diet as fed.
[8] Crude lipid: % crude lipid contained in the diet as fed.
[9] Average water temperature during a period of the growth trial.
[10] Not available: the IE value was not available because the moisture and ash contents were not recorded in the reference.

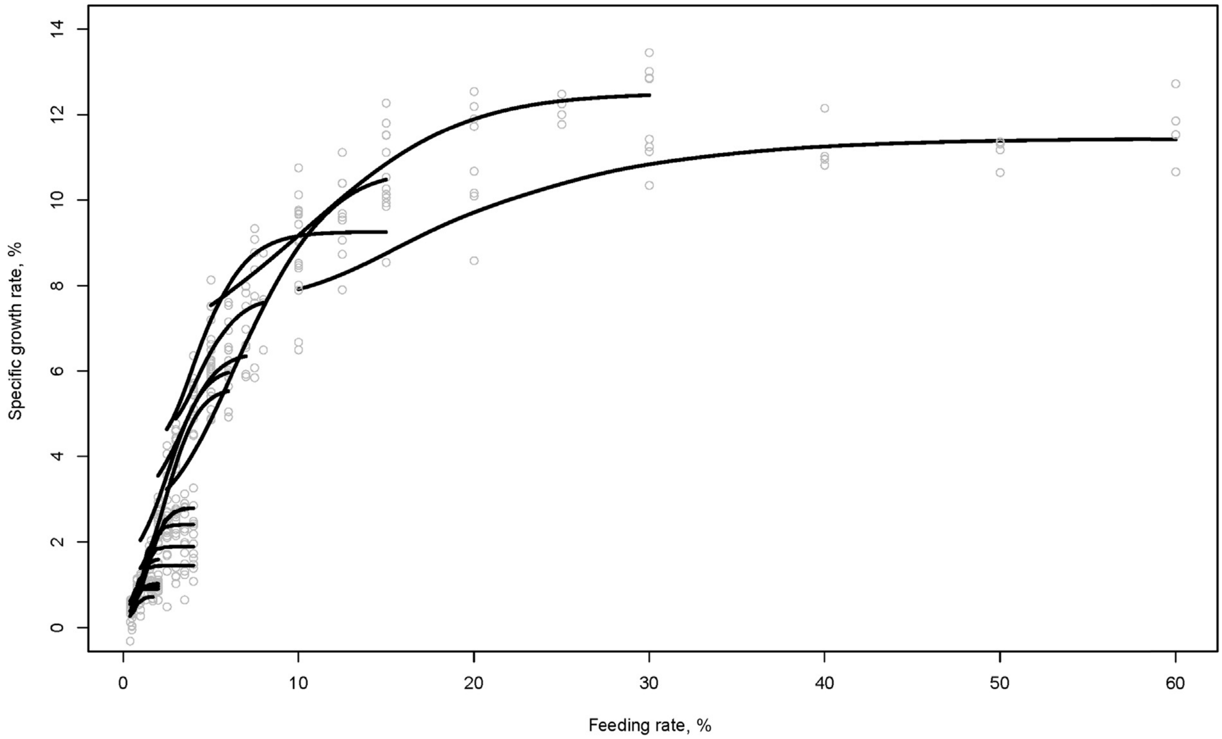

Fig. A. Logistic curve fits for the 19 datasets. The light gray circles are the original data, and the solid curves are the fits for the corresponding dataset. Note that the model for dataset 16 failed to produce an estimate because the gradient was singular when trying to use the iterative algorithm.

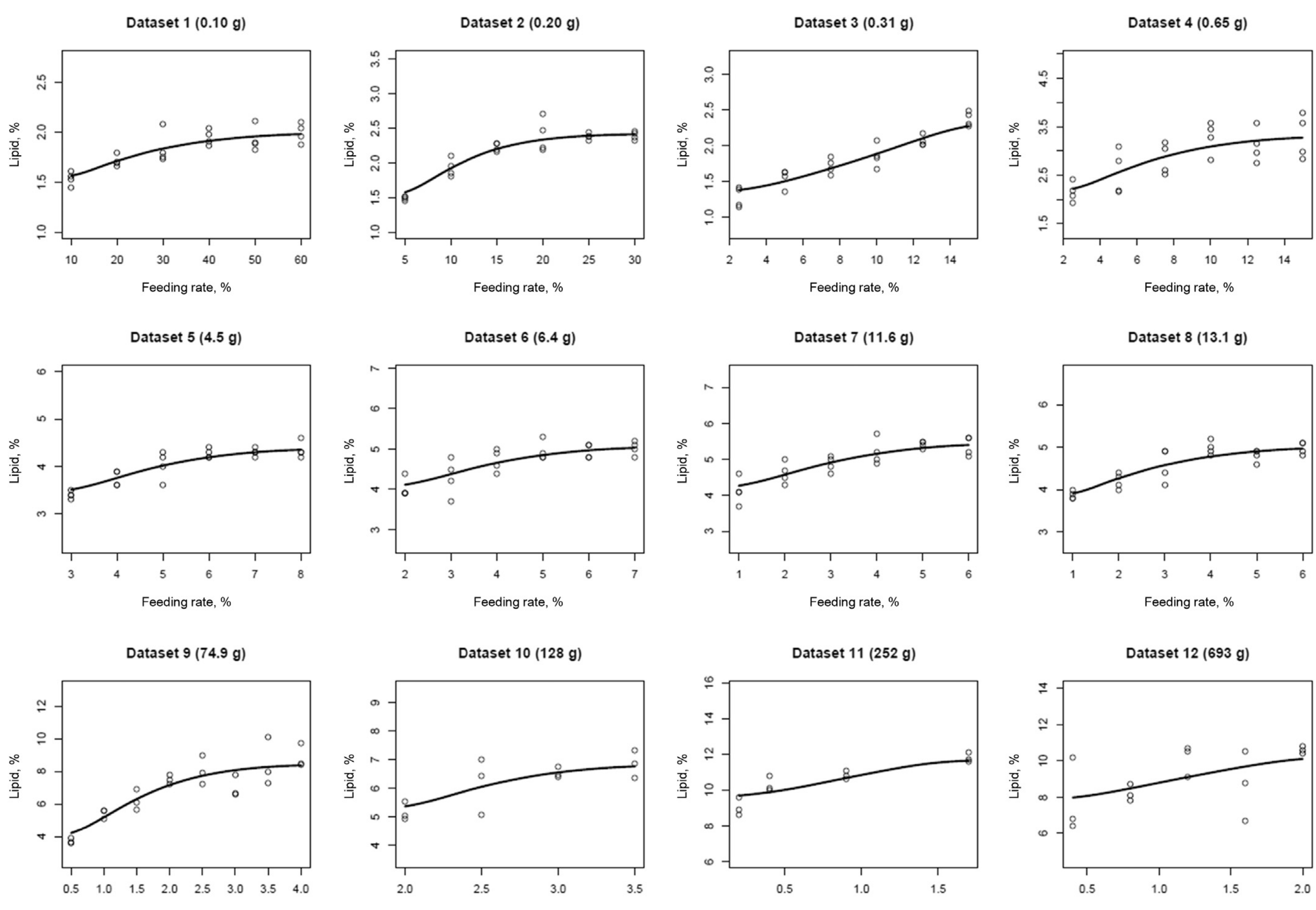

Fig. B. Logistic curve fitting for body lipid (%) as wet basis against various feeding rates (% body weight per day) tested in each of 12 datasets. Values in parentheses are average final body weights when samples were collected for proximate composition analysis.

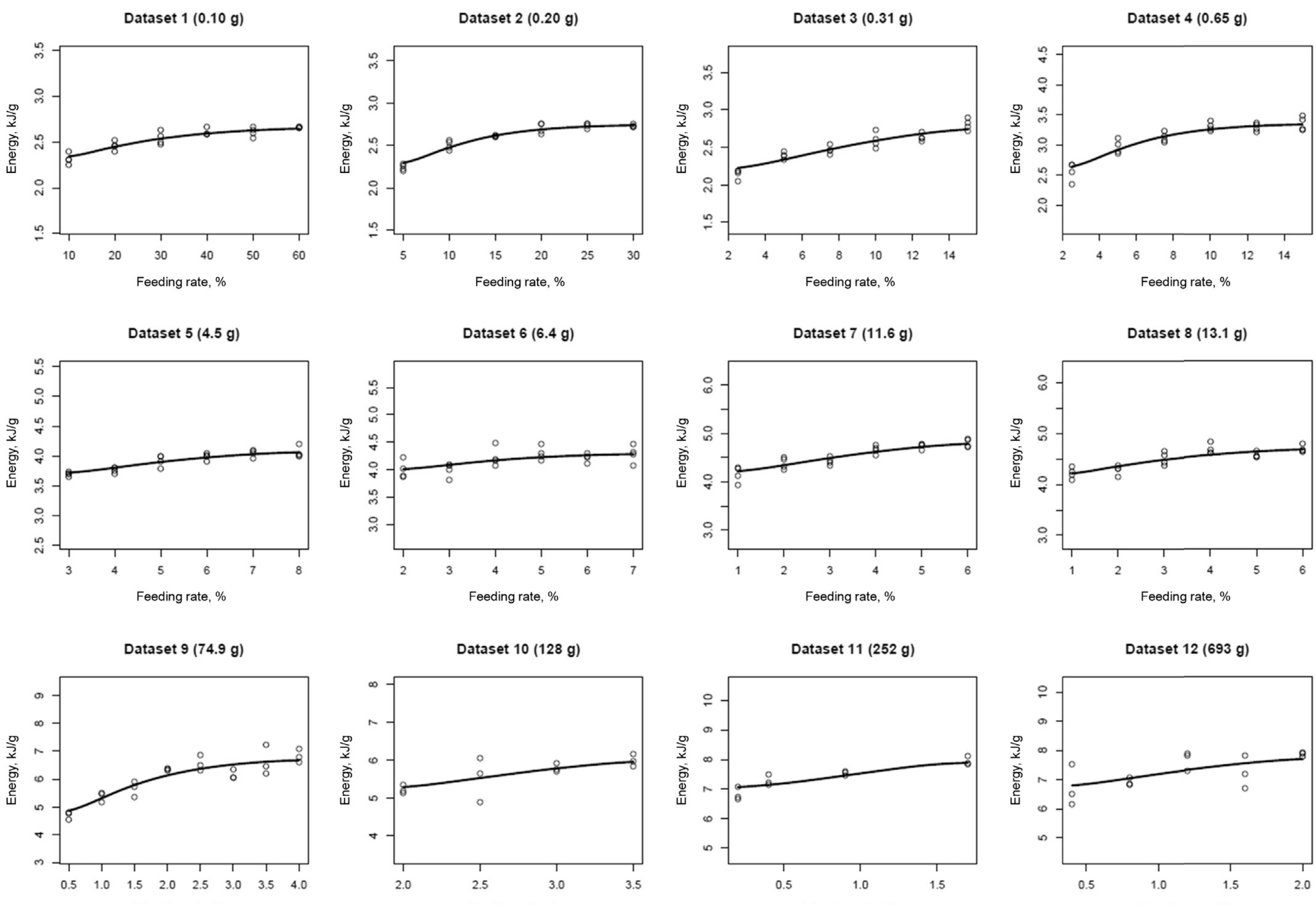

Fig. C. Logistic curve fitting for body energy (kJ/g) as wet basis against various feeding rates (% body weight per day) tested in each of 12 datasets. Values in parentheses are average final body weights (g) when samples were collected for proximate composition analysis.

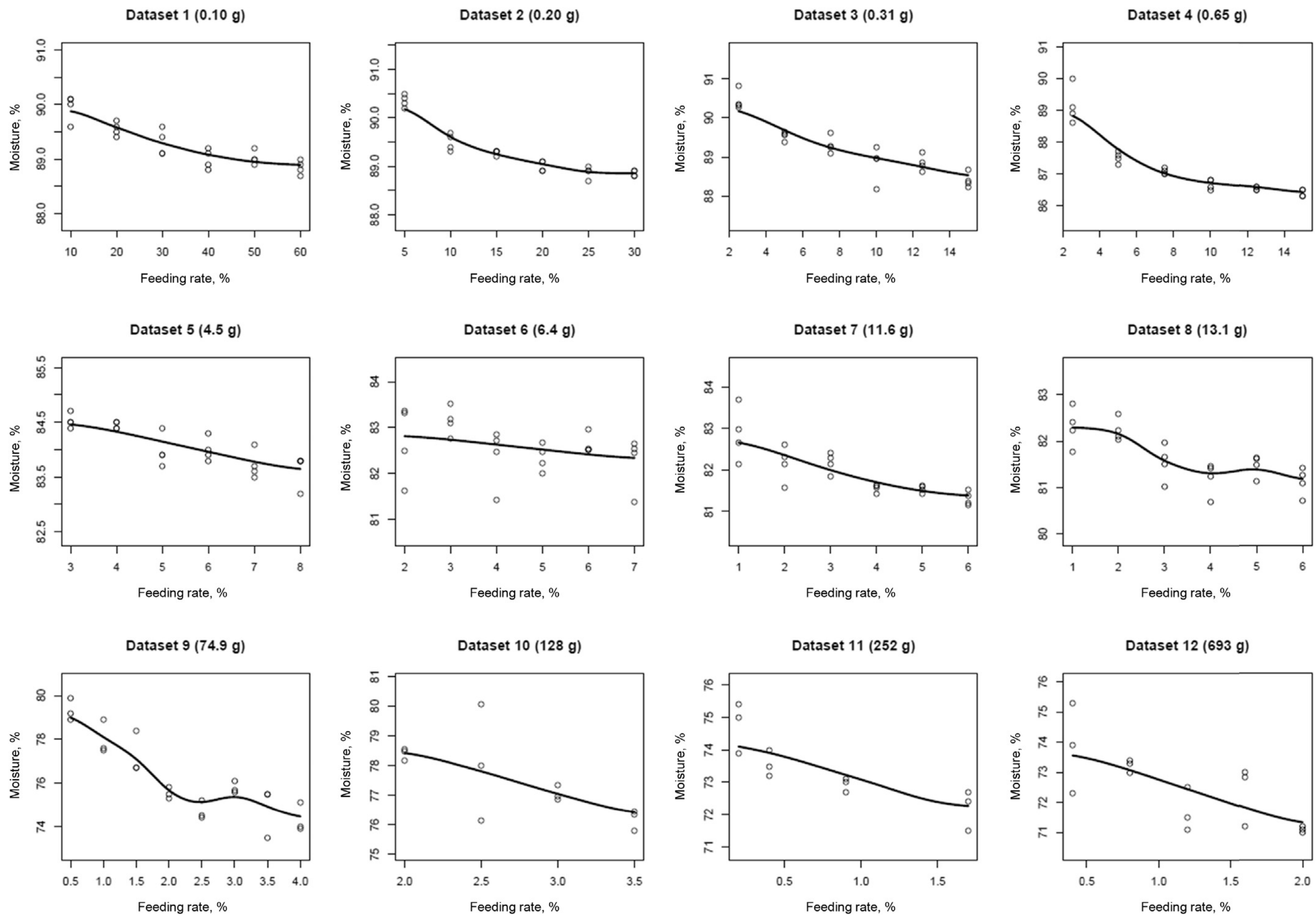

Fig. D. Polynomial fits for body moisture content (%) against various feeding rates (% body weight per day) tested in each of 12 datasets. Values in parentheses are average final body weights (g) when samples were collected for proximate composition analysis.

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